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Phylogeography and systematic notes on two species of gracile mouse opossums, genus *Gracilinanus* (Marsupialia: Didelphidae) from Brazil

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Abstract.—Although they were described more than a century ago, *Gracilinanus agilis* and *Gracilinanus microtarsus* are still mistaken for each other and their status as valid species has been challenged. Morphological studies are rare and accounts of molecular characters are even scarcer. In this paper, we present the first phylogeographic analysis for these two species based on mitochondrial cytochrome *b* sequences and provide a morphological analysis and extended diagnosis for both species. We show that *G. agilis* and *G. microtarsus* are valid species, geographically bounded and distinguishable by morphological and molecular characters. *Gracilinanus agilis* is geographicaly widespread and genetically more homogenous, with low levels of divergence between three clades in central, northeastern and eastern Brazil. *Gracilinanus microtarsus* occurs in southeastern and southern Brazil, being comprised of two clades that show a considerable level of sequence divergence. Although at this time we regard these two clades as geographic units of *G. microtarsus*, it is possible that more samples will show that there is greater diversity in this group than the current taxonomy recognizes.

The genus *Gracilinanus* (Gardner and Creighton, 1989) comprises delicately built opossums, generally smaller than individuals of *Marmosops* and *Marmosa* with which they are often confused. The dorsal coloration varies considerably, from bright reddish-brown to pale grayish-brown; the ventral pelage is often cream or pale orange with gray-based hairs, but sometimes white or pure cream as in *G. emiliae*. The tail is moderately long to very long, with non-petiolate central hairs in each caudal-scale triplet. Among diagnostic cranial characters, the more trenchant are the highly fenestrated palate, with maxillary vacuities often present, and bullae with an anteromedian strut forming a secondary foramen ovale (R. S. Voss, in litt.). Other characters and detailed descriptions of the genus can be found in Tate (1933) and Creighton (1984) under the *microtarsus* section of the formerly inclusive genus *Marmosa,* and in Gardner & Creighton (1989) and Hershkovitz (1992). Costa (in press) discusses the phylogenetic affinities of *Gracilinanus* among the didelphids, based on cytochrome *b* (cyt *b*) sequences and morphological characters.

The genus ranges from the Guiana region, through Venezuela and Colombia, bordering the western limit of the Amazon basin with scattered localities in Peru, Bolivia and Paraguay, to the mouth of the Paraná river in Argentina, then northeast along the coast and interior tablelands of Brazil, reaching the southeastern border of Amazonia. It is apparently absent from all, or at least the majority of the lowland Amazon basin in Brazil as specimens recorded from this vast region were either misidentified (see Patton et al. 2000, Voss et al. 2001) or are of questionable occurrence (Patton and Costa 2003).

Tate (1933) provided the most compre-

hensive analysis of the taxa currently included in *Gracilinanus* under the "*microtarsus* section" of his monograph. Later, Gardner & Creighton (1989) established the genus *Gracilinanus* to include six species: *G. aceramarcae* (Tate, 1931), *G. agilis* (Burmeister, 1854), *G. dryas* (Thomas, 1898), *G. emiliae* (Thomas, 1909), *G. marica* (Thomas, 1898) and *G. microtarsus* (Wagner, 1842). Yet, the number of species within the genus remains debatable since Hershkovitz (1992), in his recent revision, recognized the same six species listed above but described three new ones from the Andean slopes of Colombia (*G. longicaudus* and *G. perijae*) and Peru (*G. kalinowskii*), and recorded what he considered an undescribed additional species from Ecuador. Voss et al. (2001) subsequently defined a new genus, *Hyladelphys,* for *G. kalinowiskii.* In addition, these authors regard *G. longicaudus* as a junior synonym of *G. emiliae,* and they pointed out that Hershkovitz's undescribed "*Gracilinanus*" from Ecuador is a *Marmosa* (sensu stricto).

In the present report we address two species: *G. agilis* and *G. microtarsus.* The range of *G. microtarsus* includes the mesic habitats of the Atlantic Forest in southeastern Brazil south to Rio Grande do Sul, while *G. agilis* is more widespread in Brazil, occurring primarily in dry and gallery forests of the interior plateau, isolated areas in the Northeast, and through the wet and dry forests of northeastern Argentina, Paraguay, and Bolivia (Emmons & Feer 1997, Eisenberg & Redford 1999). Although *G. agilis* and *G. microtarsus* were described nearly 150 years ago, the lack of adequate comparisons between them has raised doubts about their validity as species. Although both Hershkovitz (1992) and Gardner (1993) recognize *G. agilis* and *G. microtarsus,* the first author suggests that *G. microtarsus* could be "no more than a subspecies of *G. agilis*", while the second author states that "the forms *agilis* and *microtarsus* may prove to be conspecific". Here we provide a phylogeographic analysis of geographic samples of both *G. microtarsus* and *G. agilis,* and present morphological comparisons and systematic comments. We also include a third species (*G. aceramarcae,* a rare opossum known only from the type locality in Bolivia [Tate 1931] and two localities in southern Peru [Eisenberg & Redford 1999; L. H. Emmons, in litt.]) in the molecular analysis to provide a more representative sampling of the taxonomic diversity within the genus.

Methods

Molecular analyses.—Our samples consist of a single specimen from Vilcabamba, Peru, tentatively identified as *G. aceramarcae,* and 34 individuals of *G. agilis* and *G. microtarsus* from 24 localities in Brazil (Fig. 1), including topotypes of *G. microtarsus* (from Ipanema, São Paulo; see Appendix). We also have samples from a locality in the same region where the type specimen of *G. agilis* was collected (Lagoa Santa, Minas Gerais).

We extracted DNA from frozen or ethanol-preserved liver tissue using the Chelex® method (Walsh et al. 1991) and amplified the cytochrome *b* (cyt *b*) gene by the Polymerase Chain Reaction (PCR), (Saiki et al. 1988) using primer pairs MVZ05 in combination with MVZ04 and/or MVZ 16. The double-strand PCR products were cleaned using the DNeasy™ Tissue Kit (QIAGEN, Inc.) and submitted to cycle sequencing reactions that utilized the dRhodamine Terminator Cycle Sequencing Kit and Protocol (PE Biosystems, Inc.), and primers MVZ05, MVZ04 and MVZ65. All sequencing was done in an ABI Prism 377 automated sequencer. Sequences were aligned by eye using Sequence Navigator (Version 1.0.1, Applied Biosystems, Inc.). The data set varied from 518 bp to 801 bp of the cyt *b* sequence, each sequence beginning with the start codon of the gene. A Nexus file of all sequences is available from the authors upon request.

Relationships among different haplotypes

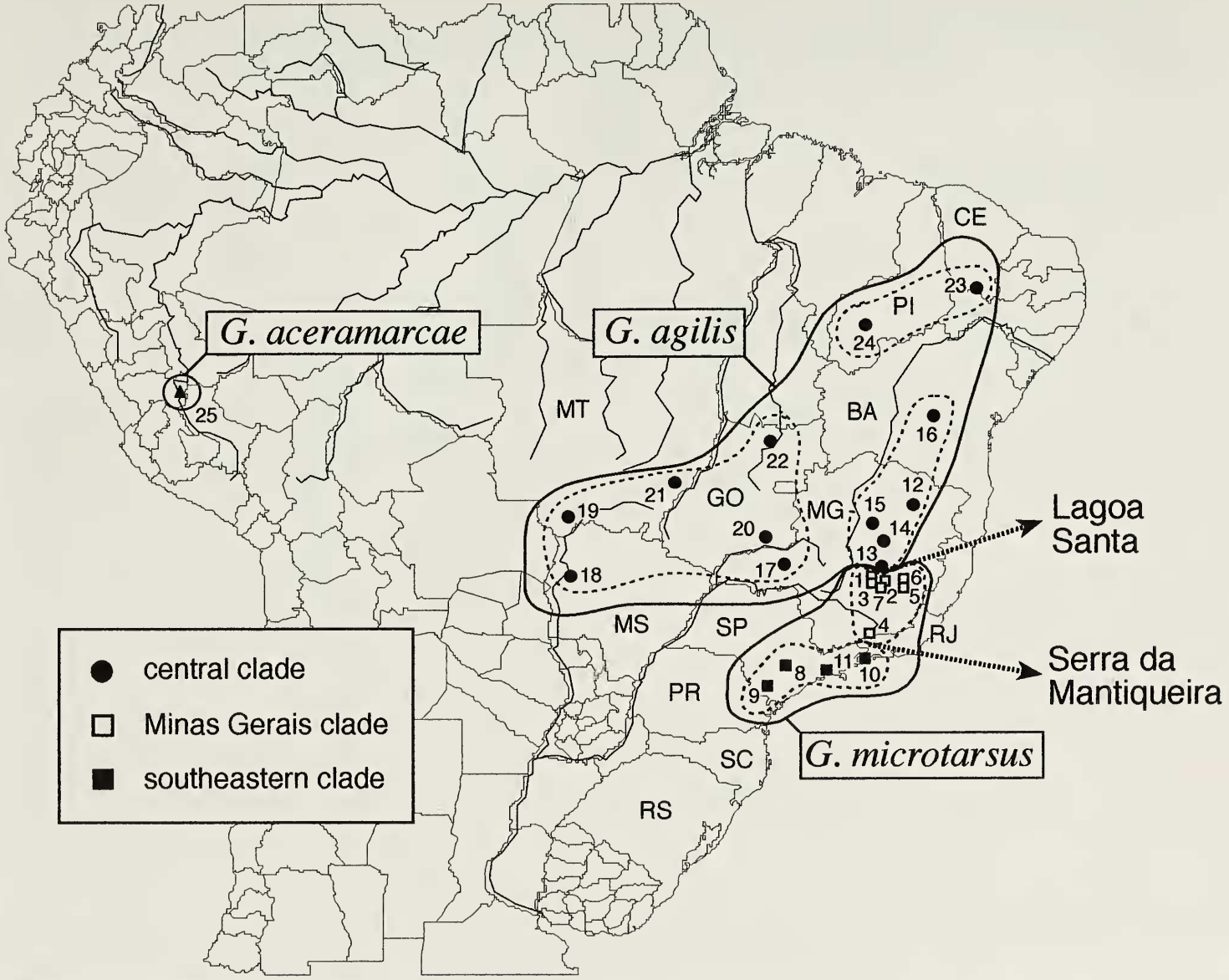

Fig. 1. Map showing the distribution of our samples and the taxa and geographic clades recognized in this report. The widespread species *Gracilinanus agilis* contacts *G. microtarsus* near Lagoa Santa, MG (locality 1; the type locality of *G. agilis*). The two clades of *G. microtarsus* are separated by the Serra da Mantiqueira mountain range. Solid lines delimit species boundaries and dashed lines indicate clades within species (see Fig. 3). Numbered localities are georeferenced in the Appendix and correspond to the same localities labeled in Fig. 3. Brazilian states are: Ceará (CE), Piauí (PI), Bahia (BA), Minas Gerais (MG), Goiás (GO), Mato Grosso (MT), Mato Grosso do Sul (MS), São Paulo (SP), Rio de Janeiro (RJ), Paraná (PR), Santa Catarina (SC), and Rio Grande do Sul (RS).

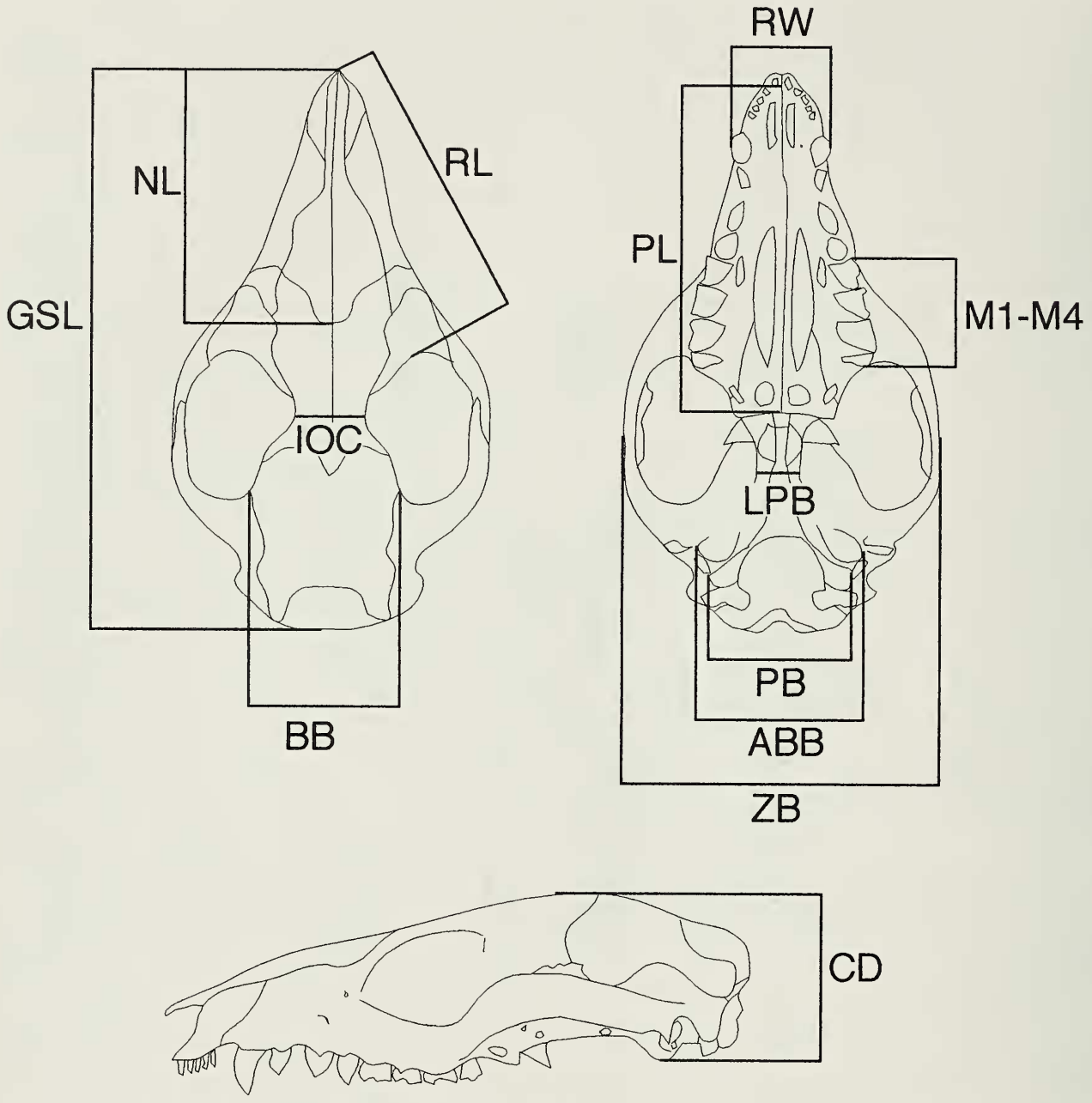

Fig. 2. Thirteen cranial measurements recorded from *G. agilis* and *G. microtarsus*, as follows: GSL—Greatest skull length: from the most anterior margin of the rostrum to the posterior margin of the occiput. ZB—Zygomatic breadth: greatest breadth across the zygomatic arches. BB (measurement 7 of Tate 1933:236)—Braincase breadth: breadth taken above the squamosal root of the zygomatic arch. IOC—Least interorbital constriction: minimal breadth across the roof of the skull above the orbits. RL—Rostral length: from the anterior margin of the orbit to the midline tip of the nasals. NL—Nasal length: midline distance from anterior tip to posterior margins of nasals. RW—Rostral width: width of the rostrum at the level of the canines. M1–M4—Molar toothrow length: taken on the labial margin of the toothrow from M1 to M4. LPB (measurement 1 of Tate 1933:236)—Least pterygoid breadth: least breadth across pterygoid bones. PB (measurement 3 of Tate 1933:236)—Petrosal breadth: breadth across tympanic process of pars petrosa. ABB (measurement 2 of Tate 1933:236)—Alisphenoid bulla breadth: breadth across tympanic processes of alisphenoid. PL—Palatal length: midline distance from the posterior margins of the first upper incisor to the posterior margin of the hard palate. CD—Cranial depth: vertical distance between ventral margins of bullae and top of cranium.

were examined by maximum parsimony using PAUP*, version 4.0b8 (Swofford 1999). Trees were constructed using the heuristic search option via stepwise addition, with 10 replicates and random sequence addition of taxa. The support for internal branches was evaluated by decay indices (Bremer 1988) and bootstrap analyses

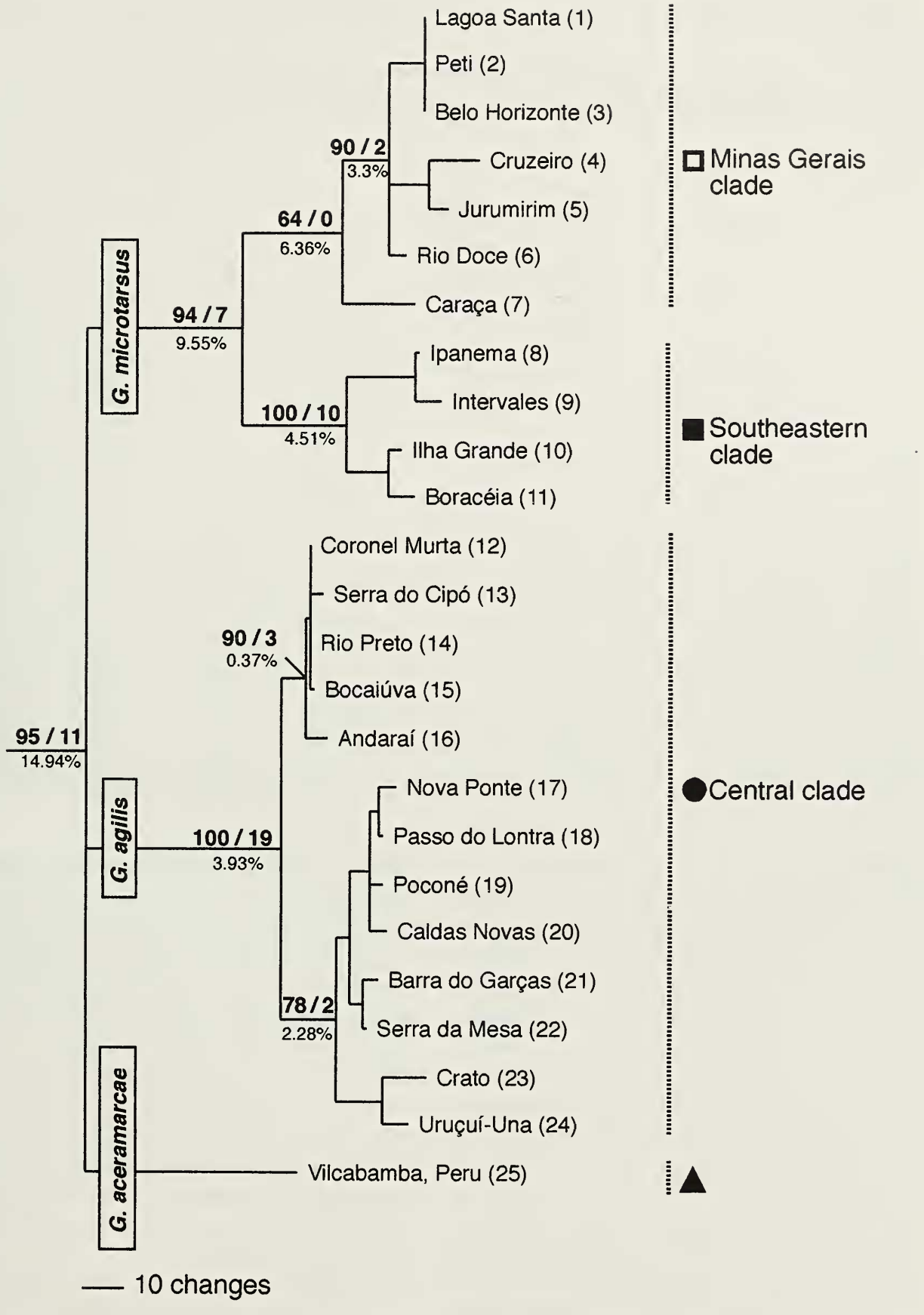

Fig. 3. Bootstrap consensus tree based on maximum parsimony analysis of cyt *b* gene haplotypes (initial 801bp). *Gracilinanus agilis* and *G. microtarsus* are reciprocally monophyletic and highly divergent species. The two clades within *G. microtarsus* are also highly divergent. Sequences of *Marmosops incanus, Thylamys* sp., and *Marmosa murina* were used as outgroups to root the tree. Bold numbers at internal nodes are bootstrap values/decay indices; percentages are average Kimura two-parameter (K2p) distances. Voucher catalog numbers and localities for each haplotype are given in the gazetteer and correspond to the same localities on the map in Fig. 1. Consistency index = 0.593; homoplasy index = 0.407; retention index = 0.761.

Table 1.—Kimura 2-parameter distances among cyt-b haplotypes of *Gracilinanus*, with *Marmosops incanus* also included.

	LC49 *M. incanus*	MNRJ31445 *G. microtarsus*	MNRJ31447 *G. microtarsus*	MCNM299 *G. microtarsus*	LC1 *G. microtarsus*	RM26 *G microtarsus*
LC49 *M. incanus*						
MNRJ31445 *G. microtarsus*	21.00%					
MNRJ31447 *G. microtarsus*	21.00%	0.00%				
MCNM299 *G. microtarsus*	19.01%	0.00%	0.00%			
LC1 *G. microtarsus*	17.91%	4.95%	4.95%	4.94%		
RM26 *G. microtarsus*	17.01%	1.98%	1.98%	2.00%	3.95%	
MCNM394 *G. microtarsus*	18.33%	2.82%	2.82%	2.80%	3.22%	3.00%
RM4 *G. microtarsus*	18.50%	6.32%	6.32%	6.37%	6.71%	5.76%
LPC805 *G. microtarsus*	20.77%	10.01%	10.01%	9.44%	9.60%	8.05%
MVZ182056 *G. microtarsus*	19.77%	10.26%	10.26%	10.21%	10.36%	9.50%
LP40 *G. microtarsus*	19.23%	8.60%	8.60%	8.59%	9.60%	8.03%
MAM427 *G. microtarsus*	20.67%	10.86%	10.86%	9.81%	10.59%	9.27%
LC189 *G. agilis*	19.02%	14.75%	14.75%	14.00%	16.56%	14.15%
MNRJ31396 *G. agilis*	18.56%	14.36%	14.36%	14.31%	15.44%	13.72%
YL64 *G. agilis*	19.03%	14.75%	14.75%	14.00%	16.56%	14.14%
LPC241 *G. agilis*	19.56%	14.76%	14.76%	14.02%	16.34%	13.93%
AP22 *G. agilis*	18.85%	14.59%	14.59%	13.80%	16.33%	13.93%
LPC304 *G. agilis*	20.53%	15.22%	15.22%	14.53%	17.16%	16.29%
LPC599 *G. agilis*	19.87%	15.23%	15.23%	14.54%	16.90%	16.03%
LPC581 *G. agilis*	19.40%	15.05%	15.05%	14.31%	16.72%	15.43%
UHECO4722 *G. agilis*	19.23%	14.73%	14.73%	14.15%	16.53%	15.25%
LPC476 *G. agilis*	18.66%	13.72%	13.72%	13.62%	14.99%	14.28%
UHESM1759 *G. agilis*	18.69%	14.58%	14.58%	13.75%	15.99%	14.79%
LPC250 *G. agilis*	19.72%	14.08%	14.08%	12.94%	14.98%	13.65%
UUP1292 *G. agilis*	19.49%	14.51%	14.51%	13.20%	15.10%	13.65%
LHE1342 *G. aceramarcae*	19.89%	15.71%	15.71%	14.28%	15.66%	13.85%

(Felsenstein 1985), with 100 bootstrap replicates each consisting of a full heuristic search as described above. On the assumption that *Gracilinanus* is monophyletic (Gardner & Creighton 1989; Voss et al. 2001), all trees were rooted by including sequences of *Marmosops incanus, Marmosa murina,* and *Thylamys* sp. as outgroups. Sequence divergence was calculated using the Kimura two-parameter algorithm (Kimura 1980) as implemented in PAUP*.

Morphological analyses.—Statistical analyses were performed using the computer package StatView (Version 5.0, SAS Institute Inc.). For analysis of external morphological data, we used 71 specimens of *G. agilis* from 10 localities, and 25 specimens of *G. microtarsus* from 9 localities in the states of São Paulo, Rio de Janeiro, and Minas Gerais (see Appendix and Fig. 1). External measurements (total length and lengths of tail, ear, and hindfoot including claws) and weight (mass) were taken from specimen labels. We subtracted tail length from total length to obtain the length of the head and body. For analyses of cranial measurement data, we examined 60 specimens of *G. agilis* and 16 of *G. microtarsus*. Each individual was classified as young or adult, adults being defined as those individuals possessing a complete set of teeth (including the permanent third premolar, and four molars). We recorded 13 cranial measurements (Fig. 2) taken with digital calipers from each individual.

Results and Discussion

Phylogenetic analysis.—The maximum parsimony analysis resulted in 80 most-parsimonious trees of 672 steps each, with 215 of the 801 characters parsimony-informa-

Table 1.—Extended.

	MCNM394 *G. microtarsus*	RM4 *G. microtarsus*	LPC805 *G. microtarsus*	MVZ182056 *G. microtarsus*	LP40 *G. microtarsus*	MAM427 *G. microtarsus*
LC49 *M. incanus*						
MNRJ31445 *G. microtarsus*						
MNRJ31447 *G. microtarsus*						
MCNM299 *G. microtarsus*						
LC1 *G. microtarsus*						
RM26 *G. microtarsus*						
MCNM394 *G. microtarsus*						
RM4 *G. microtarsus*	6.71%					
LPC805 *G. microtarsus*	9.16%	9.52%				
MVZ182056 *G. microtarsus*	9.79%	10.46%	1.34%			
LP40 *G. microtarsus*	8.24%	8.56%	3.88%	4.39%		
MAM427 *G. microtarsus*	9.64%	9.52%	4.60%	5.17%	1.43%	
LC189 *G. agilis*	14.75%	14.10%	15.98%	14.98%	14.31%	14.80%
MNRJ31396 *G. agilis*	13.88%	14.38%	14.57%	14.20%	13.50%	14.79%
YL64 *G. agilis*	14.74%	14.09%	15.97%	14.97%	14.31%	14.80%
LPC241 *G. agilis*	14.69%	13.88%	15.98%	14.97%	14.33%	15.14%
AP22 *G. agilis*	14.54%	13.87%	15.80%	14.73%	14.10%	14.64%
LPC304 *G. agilis*	15.98%	16.04%	17.85%	15.78%	14.85%	16.82%
LPC599 *G. agilis*	15.51%	15.80%	17.43%	15.76%	14.41%	16.41%
LPC581 *G. agilis*	15.71%	15.52%	16.60%	16.50%	14.58%	15.91%
UHECO4722 *G. agilis*	15.56%	15.33%	16.10%	15.82%	14.00%	15.10%
LPC476 *G. agilis*	14.04%	14.94%	15.76%	15.83%	14.62%	16.04%
UHESM1759 *G. agilis*	14.65%	14.69%	16.45%	15.84%	14.44%	15.76%
LPC250 *G. agilis*	14.01%	15.21%	16.27%	16.12%	15.11%	15.92%
UUP1292 *G. agilis*	14.43%	14.75%	16.36%	15.04%	15.09%	16.52%
LHE1342 *G. aceramarcae*	14.88%	11.76%	15.24%	16.10%	13.86%	14.68%

tive. We present only the bootstrap consensus tree (Fig. 3) since it identifies the well-supported nodes and its topology does not differ significantly from the strict consensus of the most-parsimonious trees. A matrix of Kimura 2-parameter (K2p) distances among the 25 unique haplotypes of *Gracilinanus,* plus *Marmosops incanus,* is given in Table 1.

The bootstrap tree (Fig. 3) shows a basal, unresolved trichotomy between the *G. aceramarcae* sample, a clade from central Brazil (Figs. 1 and 3; localities 1–11), and a third clade formed by two groups from eastern Brazil (Figs. 1 and 3; localities 12–24). These three clades are highly divergent from each other, differing by an average K2p distance of about 15%. The two clades from eastern Brazil [Minas Gerais (localities 1–7; Fig. 1) and Southeastern clades (localities 8–11)] are also quite divergent (average K2p value of 9.55%), remarkably so considering the small geographic distances separating them. On the other hand, there is a surprisingly amount of homogeneity among the samples of the Central clade since its representatives come from widely separated localities but are only 3.93% divergent on average. Yet, the Central clade is divided into sub-clades: a more divergent one encompassing the northern part of Minas Gerais and central Bahia (localities 12–16; Fig. 1), another in the Northeast (localities 23–24), and a wide-spread third in central Brazil in the states of Mato Grosso, Mato Grosso do Sul, Goiás and western Minas Gerais (localities 17–22).

The bootstrap tree and the strict consensus of the parsimony trees differ only in the placement of two samples. First, *G. aceramarcae* is sister to *G. agilis* and *G. microtarsus* in the strict consensus tree, but with

Table 1.—Extended.

	LC189 *G. agilis*	MNRJ31396 *G. agilis*	YL64 *G. agilis*	LPC241 *G. agilis*	AP22 *G. agilis*	LPC304 *G. agilis*
LC49 *M. incanus*						
MNRJ31445 *G. microtarsus*						
MNRJ31447 *G. microtarsus*						
MCNM299 *G. microtarsus*						
LC1 *G. microtarsus*						
RM26 *G. microtarsus*						
MCNM394 *G. microtarsus*						
RM4 *G. microtarsus*						
LPC805 *G. microtarsus*						
MVZ182056 *G. microtarsus*						
LP40 *G. microtarsus*						
MAM427 *G. microtarsus*						
LC189 *G. agilis*						
MNRJ31396 *G. agilis*	0.60%					
YL64 *G. agilis*	0.00%	0.60%				
LPC241 *G. agilis*	0.76%	1.00%	0.76%			
AP22 *G. agilis*	0.13%	0.84%	0.13%	0.88%		
LPC304 *G. agilis*	4.49%	3.31%	4.49%	4.83%	4.66%	
LPC599 *G. agilis*	4.01%	3.07%	4.01%	4.34%	4.18%	0.77%
LPC581 *G. agilis*	3.47%	3.19%	3.48%	3.74%	3.61%	1.22%
UHECO4722 *G. agilis*	3.34%	3.28%	3.34%	3.88%	3.47%	0.93%
LPC476 *G. agilis*	3.33%	3.13%	3.33%	3.30%	3.57%	2.30%
UHESM1759 *G. agilis*	3.48%	3.06%	3.48%	3.75%	3.61%	2.01%
LPC250 *G. agilis*	4.82%	4.94%	4.82%	5.38%	4.96%	4.95%
UUP1292 *G. agilis*	4.30%	3.99%	4.31%	4.85%	4.44%	3.79%
LHE1342 *G. aceramarcae*	13.26%	14.84%	13.26%	13.59%	13.11%	14.67%

low support (bootstrap < 50%), while the three form an unresolved polytomy in the bootstrap tree (Fig. 3). Second, in the strict consensus tree, the Caraça sample (locality 7; Fig. 1) falls in a trichotomy with the Southeastern and Minas Gerais clades, while in the bootstrap tree it joins the Minas Gerais clade, but again with low support (bootstrap = 64%; decay index = 0) and high sequence divergence (6.4% on average; Fig. 3). The ambiguous position of the Caraça sample and the degree of divergence separating it from the remaining samples highlight its uniqueness and indicates that populations from this mountain range might have been isolated for a considerable period of time.

Taxon allocation of the phylogeographic clades.—We identify three phylogeographic clades of *Gracilinanus* in eastern and central Brazil: Southeastern, Minas Gerais, and Central clades (Fig. 1). The Southeastern clade includes a specimen from Ipanema, the type locality of *G. microtarsus* (locality 8; Fig. 1; Appendix) and for that reason, as well as by comparison to the description of the holotype given by Tate (1933:191), we refer it to this species. The allocation of names to the two other clades, however, is more complicated. The name *G. agilis* has been historically applied to populations in central Brazil, from the state of Ceará in northeastern Brazil southwest to Lagoa Santa, and then continuing southwest, but interior to the coastal regions of São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul, to the Chaco of Paraguay and Argentina (Tate 1933). This range matches the distribution of our samples from the Central clade. However, the Minas Gerais clade includes a specimen from Lagoa Santa (locality 1; Fig. 1), the type locality of *G. agil-*

Table 1.—Extended.

	LPC599 *G. agilis*	LPC581 *G. agilis*	UHECO4722 *G. agilis*	LPC476 *G. agilis*	UHES1759 *G. agilis*	LPC250 *G. agilis*	UUP1292 *G. agilis*
LC49 *M. incanus*							
MNRJ31445 *G. microtarsus*							
MNRJ31447 *G. microtarsus*							
MCNM299 *G. microtarsus*							
LC1 *G. microtarsus*							
RM26 *G. microtarsus*							
MCNM394 *G. microtarsus*							
RM4 *G. microtarsus*							
LPC805 *G. microtarsus*							
MVZ182056 *G. microtarsus*							
LP40 *G. microtarsus*							
MAM427 *G. microtarsus*							
LC189 *G. agilis*							
MNRJ31396 *G. agilis*							
YL64 *G. agilis*							
LPC241 *G. agilis*							
AP22 *G. agilis*							
LPC304 *G. agilis*							
LPC599 *G. agilis*							
LPC581 *G. agilis*	0.45%						
UHECO4722 *G. agilis*	0.79%	0.88%					
LPC476 *G. agilis*	2.07%	2.05%	2.16%				
UHESM1759 *G. agilis*	1.55%	1.26%	1.39%	1.10%			
LPC250 *G. agilis*	4.47%	3.88%	3.75%	5.07%	3.62%		
UUP1292 *G. agilis*	3.31%	3.10%	2.97%	3.24%	2.84%	2.04%	
LHE1342 *G. aceramarcae*	14.68%	14.38%	13.74%	15.83%	14.39%	14.38%	15.11%

is, which is situated on the border with the Central clade. To resolve this problem, we compared our specimens with the descriptions of each holotype. If our specimen from Lagoa Santa is the same as Burmeister's type of that taxon, then *G. agilis* would become the name available for the Minas Gerais clade, recognized either as a separate species, or as a synonym of *G. microtarsus.* In either case, the Central clade, which we identify, would require another name, presumably one of those currently listed as synonyms of *G. agilis.* On the other hand, if the type specimen of *G. agilis* matches the morphology of the specimens from the Central clade, then we are left with a decision to make about the Minas Gerais clade, which could be recognized as a more interior clade of *G. microtarsus* or a separate, undescribed species, by virtue of its high level of divergence from topotypic *G. microtarsus.*

The type of *G. agilis* is a young adult from Lagoa Santa, collected by H. Burmeister and deposited at the Zoologisch Museum in Halle, Germany. The skin is mounted and the skull is in fragments, with only the rostrum and palate intact (Tate 1933: Plate 24, photo 215). Since we have not seen the type material of *G. agilis,* the best we can do at present is to follow Tate's (1933) diagnosis. The following is his description (p. 195) of the type of *G. agilis*: "Skin of type very faded brown. The hair rather close and even in length. Chest and posterior parts gray-based; throat and neck with self-colored hairs, buff-white. Vibrissae short; eye-rings elongate before and behind, narrowed above and below. Feet small. Tail thickly covered with fine hair."

Table 2.—Means (±*SE*) and ranges for selected external and cranial variables of *G. agilis* and *G. microtarsus*[a]. Weight in grams, measurements in millimeters.

Character	*Gracilinanus agilis*				*Gracilinanus microtarsus*		
	Male		Female		Male		Female
Head and body length	100.0 ± 7.06	***	89.63 ± 7.28	**	104.0 ± 14.55	ns	95.20 ± 16.86
	82–115		81–108	ns	86–129		81–116
	n = 44		n = 27		n = 20		n = 5
Tail length	137.91 ± 9.30	***	123.96 ± 7.54	***	154.20 ± 7.13	**	140.20 ± 9.34
	110–158		110–139	***	139–167		131–155
	n = 43		n = 27		n = 20		n = 5
Hind foot length	16.86 ± 0.98	***	15.63 ± 1.21	*	17.95 ± 1.39	*	15.80 ± 0.84
	15–19		13–18	ns	15–20		15–17
	n = 44		n = 27		n = 20		n = 5
Ear length	22.39 ± 1.32	**	21.52 ± 1.01	**	20.60 ± 1.23	*	19.20 ± 0.84
	20–25		20–24	**	19–23		18–20
	n = 44		n = 27		n = 20		n = 5
Mass (g)	23.56 ± 6.01	***	16.15 ± 2.96	**	27.40 ± 10.62	ns	22.40 ± 10.74
	15–40		13–25	**	17–52		12–37
	n = 44		n = 27		n = 20		n = 5
Greatest skull length	28.47 ± 1.07	***	26.95 ± 1.08	***	30.27 ± 1.54	*	28.29 ± 1.48
	25.87–30.59		25.23–29.69	*	28.16–33.20		26–80
	n = 36		n = 24		n = 12		29.75
							n = 4
Zygomatic breadth	15.49 ± 0.66	***	14.63 ± 0.70	**	16.37 ± 1.13	ns	15.51 ± 1.24
	14.32–17.00		13.68–16.65	*	14.77–18.38		14.28–16
	n = 35		n = 24		12		99
							n = 4
Braincase breadth	11.40 ± 0.32	***	11.04 ± 0.33	***	11.94 ± 0.20	*	11.63 ± 0.20
	10.75–11.91		10.23–11.59	**	11.30–12.25		11.35–11.80
	n = 36		n = 24		n = 12		n = 4
Least interorbital constriction	4.67 ± 0.22	**	4.46 ± 0.22	***	5.24 ± 0.34	ns	4.98 ± 0.28
	4.20–5.06		3.96–4.86	**	4.73–5.93		4.70–5.29
	n = 36		n = 24		n = 12		n = 4
Rostral length	10.75 ± 0.53	***	10.17 ± 0.49	***	11.55 ± 0.79	*	10.59 ± 0.96
	9.29–11.56		9.28–11.03	ns	10.30–12.98		9.68–11.45
	n = 36		n = 24		n = 12		n = 4
Nasal length	12.17 ± 0.61	***	11.39 ± 0.74	**	12.98 ± 1.04	ns	12.13 ± 1.40
	10.32–13.37		10.22–13.18	ns	11.22–14.52		10.61–13.63
	n = 36		n = 24		n = 12		n = 4
Rostral width	4.49 ± 0.23	***	4.21 ± 0.26	*	4.69 ± 0.36	ns	4.43 ± 0.39
	4.03–4.98		3.74–4.75	ns	4.32–5.46		4.03–4.85
	n = 36		n = 24		n = 12		n = 4
Molar toothrow length	5.49 ± 0.16	ns	5.41 ± 0.15	***	5.73 ± 0.19	ns	5.66 ± 0.20
	5.19–5.83		5.12–5.63	**	5.50–6.07		5.42–5.90
	n = 36		n = 24		n = 12		n = 4
Least pterygoid breadth	3.02 ± 0.21	ns	2.93 ± 0.20	***	3.32 ± 0.14	ns	3.36 ± 0.11
	2.36–3.44		2.59–3.34	**	3.11–3.59		3.25–3.48
	n = 36		n = 24		n = 12		n = 4
Petrosal breadth	8.34 ± 0.25	**	8.17 ± 0.20	***	8.78 ± 0.32	ns	8.63 ± 0.38
	7.81–8.84		7.79–8.45	**	8.0–9.16		8.12–9.01
	n = 36		n = 24		n = 12		n = 4
Alisphenoid bulla breadth	9.12 ± 0.28	ns	8.96 ± 0.33	***	9.61 ± 0.25	ns	9.31 ± 0.31
	8.56–9.82		8.15–9.35	ns	9.12–10.04		9.04–9.72
	n = 35		n = 24		n = 11		n = 4
Palatal length	13.89 ± 0.56	***	13.06 ± 0.67	***	14.70 ± 0.83	*	13.75 ± 0.93
	12.68–14.95		12.08–14.39	ns	13.11–16.08		12.75–14.57
	n = 36		n = 23		n = 12		n = 4

Table 2.—Continued.

Character	*Gracilinanus agilis*				*Gracilinanus microtarsus*			
	Male		Female		Male		Female	
Cranial depth	9.61 ± 0.31	**	9.39 ± 0.34	**	9.97 ± 0.33	*	9.57 ± 0.18	
	8.80–10.10		8.63–9.84	ns	9.41–10.52		9.34–9.74	
	n = 36		n = 24		n = 12		n = 4	

[a] Mean and standard deviation, with range below, for adult specimens of both sexes. The significance levels between males and females of each species and between the two species for both males (above) and females (below) are indicated: ns = $p > 0.05$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

He then (p. 195) gives a more complete description of a specimen from Sapucay, Paraguay deposited at the British Museum (now Natural History Museum of London; BM 3.4.7.22): "Dorsal color a dull, almost dusty shade, nearest to russet (R.) or Brussels brown (R.). Color ventrally between warm buff (R.) and cinnamon-buff (R.). Gray-based hairs throughout, except from upper chest to chin and around the scrotal region. Face not markedly paler than dorsum; ears large, light gray-brown; vibrissae short; feet rather pale; tail very slightly bicolor, brown." Finally, in comparison with *G. microtarsus,* Tate wrote (p. 191): "*Microtarsus* is much more vividly colored than *agilis,* and the spreading of the gray-based hairs completely across the ventral area, except for the chin, affords another probably constant difference."

Tate's description of *G. agilis* fits quite well the individuals from the Central clade, especially the appearance and color of the dorsal pelage, the lack of strong contrast between face and dorsum, and in the extent to which the gray-based hairs cover the ventral region. All seven specimens examined from the Minas Gerais clade—including the individual from near the type locality of *G. agilis* at Lagoa Santa (MNRJ 31445)—are warm-brown on the dorsum with a much paler face, and gray-based hairs cover most of the underparts, except the chin. These are features that characterize individuals of *G. microtarsus.* In contrast, all 62 specimens of the Central clade are grayish-brown and without a sharp distinction between face and dorsum. The gray-based hairs in the underparts are restricted to the lower pectoral and abdominal area leaving upper chest, throat and chin covered with self-colored hairs (same color from base to tip). These and other traits (discussed below) convince us that the specimens forming the Central clade correspond to *G. agilis.* Despite the high genetic divergence found between the Southeastern clade and the Minas Gerais clade (Fig. 3), and the clear geographic break separating them (Serra da Mantiqueira; Fig. 1), at this time we allocate the Minas Gerais clade also to *G. microtarsus,* since we could find no diagnostic morphological characters that justify specific distinction. Nevertheless, we point out that our sample size of *G. microtarsus* is small and it is possible that more individuals will provide the morphological support for distinction at the species level. It is important to note that *G. agilis* and *G. microtarsus* occur in near-sympatry in the state of Minas Gerais, since both species are now known from the general vicinity of Lagoa Santa. This locality is in a contact area between two biomes: the Cerrado, which has savanna-like vegetation characteristic of central Brazil, and the Atlantic Forest, represented at Lagoa Santa by semi-deciduous forests. Based on current distributional information, *Gracilinanus agilis* occurs primarily in the Cerrado domain, while *G. microtarsus* is an Atlantic Forest species.

In the following section we compare the two species and give an extended description of both *G. agilis* and *G. microtarsus.*

Morphological comparisons.—External body measurements: *Gracilinanus agilis* is sexual dimorphic, as males are significantly

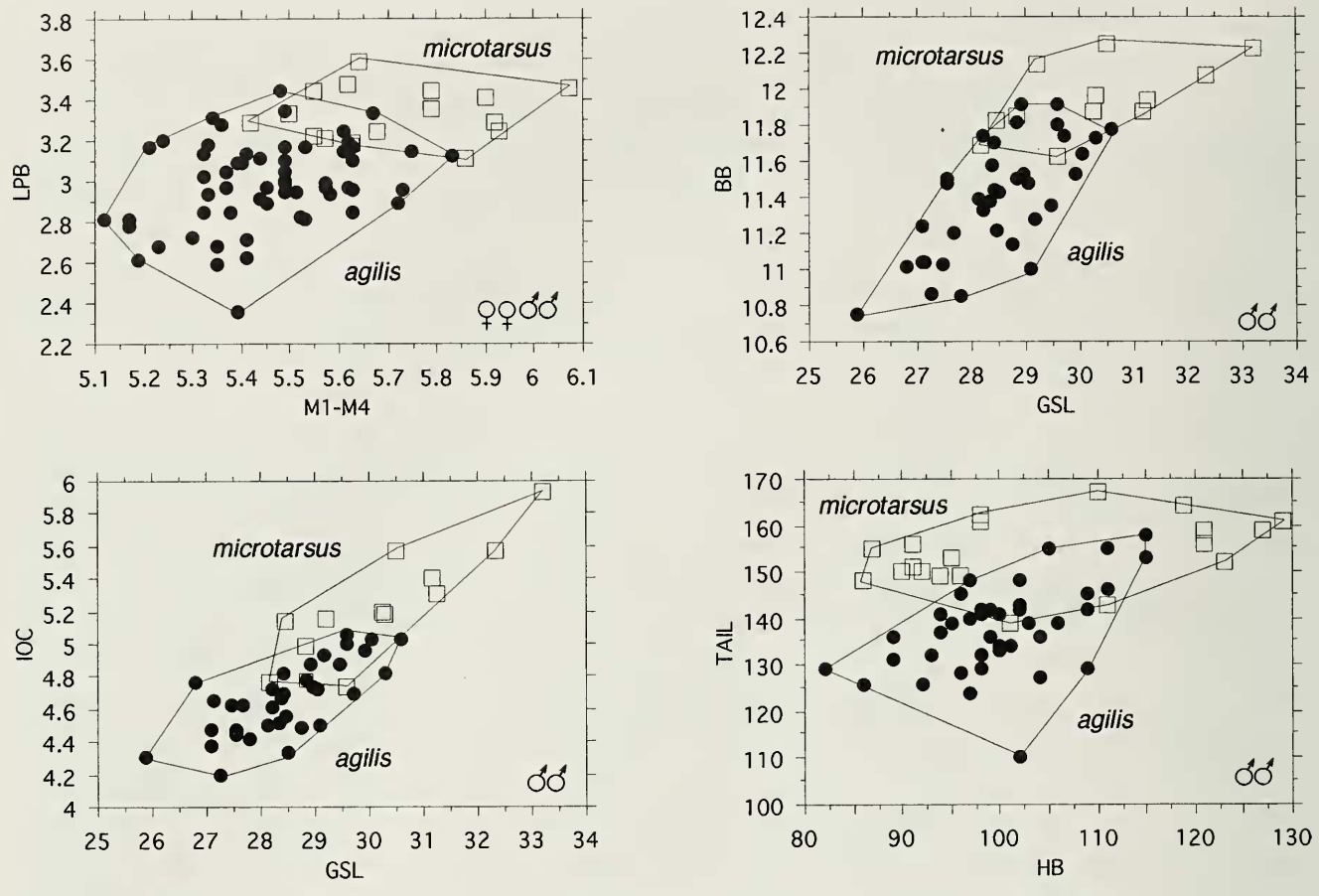

Fig. 4. Bivariate plots comparing selected external body and craniodental measurements of *Gracilinanus agilis* (open squares) and *G. microtarsus* (solid circles). Above left: molar toothrow length (M1–M4) versus least pterygoid breadth (LPB) of males and females. Above right: greatest skull length (GSL) versus braincase breadth (BB) of males. Below left: GSL versus least interorbital constriction (IOC) of males. Below right: head and body length (HB) versus tail length (TAIL) of males.

larger than females in every trait examined (see Table 2). Adult males range in head and body length from 82 to 115 mm and weigh from 15 to 40 g. Females range in head and body length from 81 to 108 mm and weigh from 13 to 25 g. The tail is longer in males, reaching 158 mm, while in females the tail reaches a maximal length of 139 mm. The ears of *G. agilis* are large, averaging more than 21 mm in both sexes. In *G. microtarsus* the tail, foot, and ears are longer in males than in females, while head and body and weight do not differ significantly (Table 2). In comparison, *G. agilis* is generally smaller than *G. microtarsus,* with females of *G. microtarsus* almost as heavy as males of *G. agilis,* and males of *G. microtarsus* approximately 17% heavier on average than males of *G. agilis.* The tail in *G. microtarsus* is also longer, by about 11% more in both sexes (Table 2; Fig. 4). The ears are the only trait that is larger in *G. agilis* than in *G. microtarsus,* which may be related to the warmer and drier habitats this species occupies.

Pelage differences: In both species, the bases of the hairs on the upper parts are dark gray and the tips are orange to buffy. However, in *G. agilis* the terminal (orange or buffy) portion of each hair is shorter than in *G. microtarsus,* giving the dorsal pelage a more grizzled tone, while *G. microtarsus* has a more uniformly colored reddish-brown pelage (Fig. 5; Table 3). The general color of the dorsal pelage is also paler in *G. agilis* than in *G. microtarsus* (Fig. 5). The fur is slightly longer and more lax in *G. microtarsus* than in *G. agilis,* although the series of *G. microtarsus* from Ipanema have the shortest fur of all specimens examined. Although Tate (1933) emphasized the presence of numerous over-hairs in *G.*

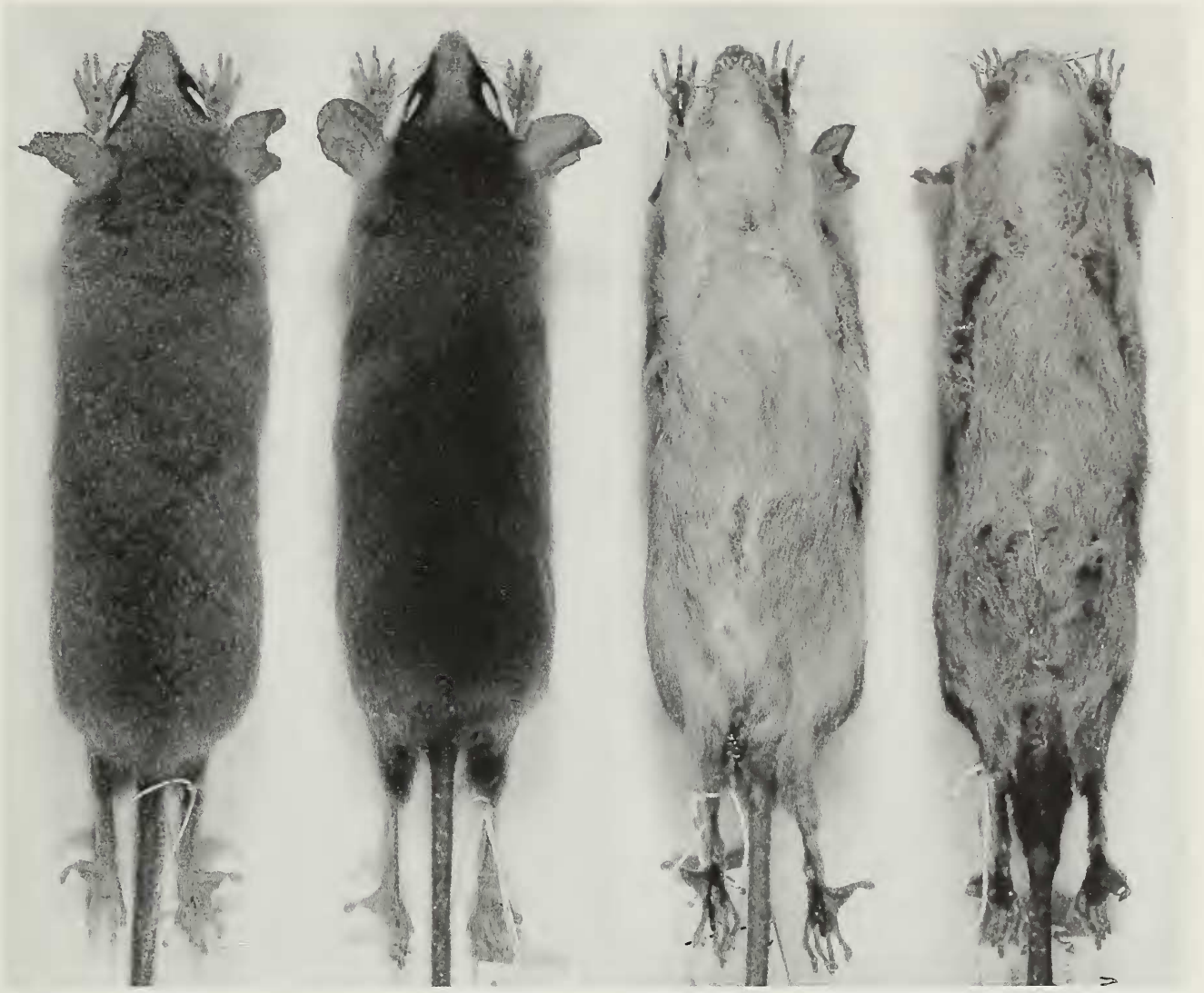

Fig. 5. Differences in dorsal and ventral color patterns of *Gracilinanus agilis* and *G. microtarsus*. *Gracilinanus agilis*: first (LPC 599) and third (LPC 581) from left; and *G. microtarsus*: second (LPC 805) and fourth (LC 1) from left. Note the grizzled and paler dorsal pelage of *G. agilis*, and the ventral gray-based hairs extending to the throat in *G. microtarsus*. Note also the sharp contrast between face and body in *G. microtarsus*, and the gradual change in *G. agilis*.

microtarsus, making the pelage "rough or shaggy-looking", our specimens appear smooth-coated.

The general color of the ventral fur is yellowish cream in both species, but as mentioned above, the gray-based hairs of *G. agilis* are restricted to the lower pectoral and abdominal area, leaving the upper chest, throat and chin self-colored (Fig. 5). Also, the gray tone on the venter is slightly paler than that of the dorsum, making the gray color less evident. Individuals from the two more interior clades of *G. agilis* have the underparts of the arms also self-colored. *Gracilinanus microtarsus*, in turn, has gray-based hairs throughout the ventral parts, except on the chin (Fig. 5), and the gray tone of the venter is as dark as it is in the dorsum, making it obvious. Apparently, the population of *G. microtarsus* in the type locality is an exception to this generality. Among the series of six topotypes we collected, one individual has the self-colored area restricted to the chin; three individuals have the self-colored hairs reaching the upper chest; and the last individual has the self-colored hairs reaching as far as the lower abdominal area. Tate's description (1933:191) of the type specimen of *microtarsus* is "Underparts cinnamon-buff, the

Table 3.—Diagnostic characters of *G. agilis* and *G. microtarsus*.

Character	*G. agilis*	*G. microtarsus*
External		
appearance of dorsum pelage	grizzly grayish-brown	uniform reddish-brown
spreading of gray-based hairs across the ventral area	throughout, except from upper chest to chin (underparts of arms also often self-colored)	variable, but usually throughout except for the chin
ocular-mark	thin, small and not extending to nose and ears	broad, large, and extending to nose and ears
face	not markedly paler than dorsum; transition is gradual, not sharp contrast with the rest of body	markedly paler than dorsum, producing a sharp contrast with the rest of body
ears	larger; >21 mm in average	smaller; <21 in average
tail	shorter; <140 mm in average	longer; >140 mm in average
Cranial		
posterolateral vacuities on palate	size larger or comparable to that of the posteromedial vacuities	always smaller than posteromedial vacuities

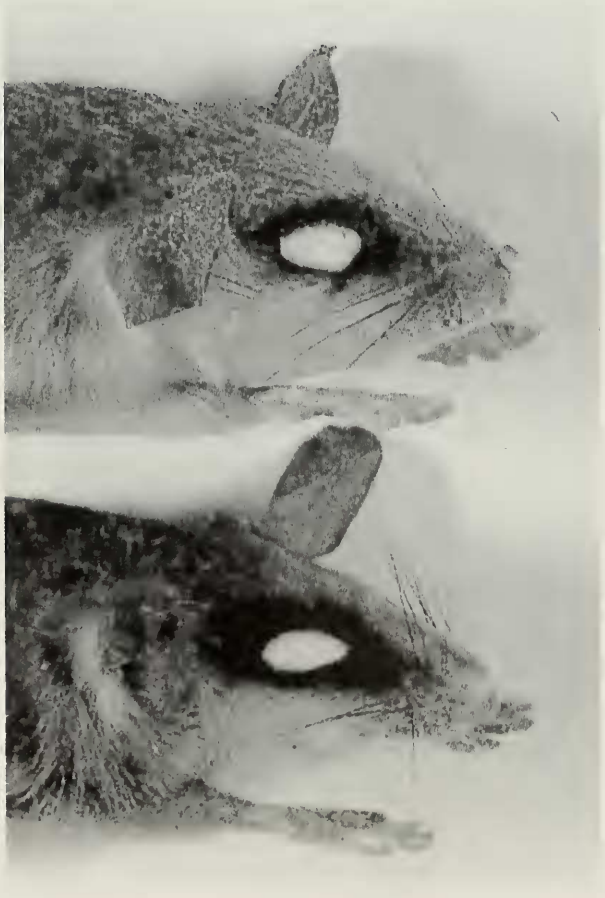

Fig. 6. Side view of the heads of *Gracilinanus agilis,* above (LPC 599), and *G. microtarsus,* below (LPC 805), showing the differences in size and shape of the ocular mask.

hairs gray-based, and only those of the chin self-colored", although he also recognized some variation since on page 189 he wrote: "underparts, posterior to the throat, with the hairs entirely gray-based". Intraspecific variation is also found in *G. agilis*: the series of 13 individuals from Crato (locality 23) are even paler than the remaining specimens of this species, the color of the dorsal region approximating a grayish tone and the self-colored parts in the underparts being whitish cream.

The ocular ring in *G. microtarsus* is broad and very dark (Fig. 6); the face is distinctly paler than the body—approximately the same color as the cheeks—resulting in a sharp contrast between the face and body (Fig. 5). Although the mask is also prominent in *G. agilis,* it is thinner and antero-posteriorly restricted (Fig. 6); the face is not as pale—the color on top of the head is darker than the cheeks—and the transition between the face and body is gradual (Fig. 5).

Cranial differences: When comparing *G. microtarsus* and *G. agilis* Tate (1933:191) observed that "The skulls are extremely alike, differing solely in finer detail". The only differences he pointed out were the

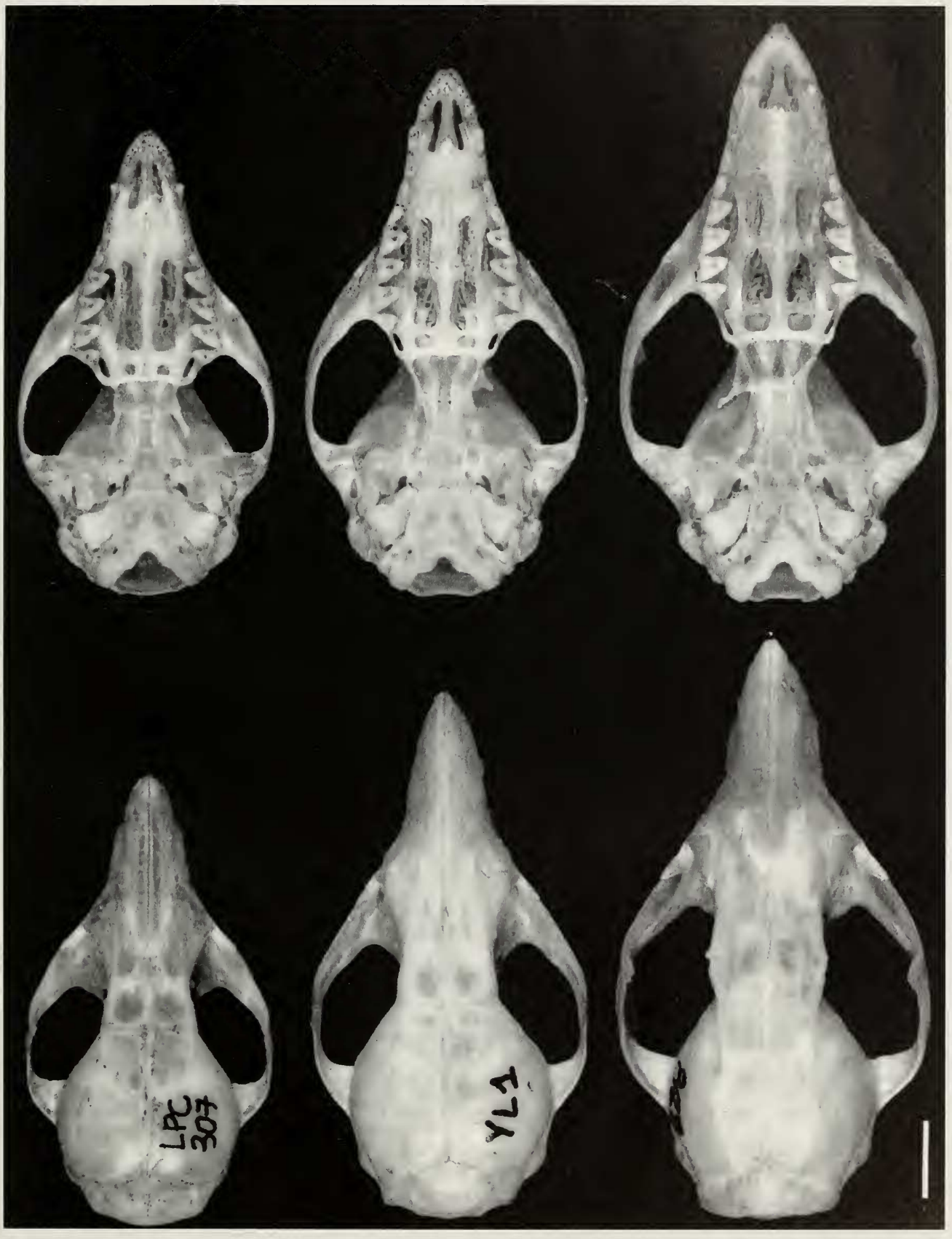

Fig. 7. Ventral and dorsal views of skulls of *Gracilinanus agilis* to the left (LPC 307, from Nova Ponte, Minas Gerais), *G. microtarsus* from the Minas Gerais clade (YL 1, from Santa Rita de Jacutinga, Minas Gerais) in the middle, and a topotype of *G. microtarsus* from the Southeastern clade to the right (MVZ 197436, from Ipanema, São Paulo). Scale bar = 5 mm. Note the larger posterolateral palatal foramina in *G. agilis*, when compared to the size of the posteromedial vacuities.

longer tooth rows of *G. microtarsus,* its somewhat broader and shorter pterygoids and proportionately greater breadth across the pars petrosa. While we confirmed Tate's findings with confidence for both males and females (Table 2; Fig. 4), we also detected additional differences. Skulls of *G. microtarsus* are longer (Figs. 4 and 7), and they also have a wider braincase, wider zygomatic arches, and broader interorbital region (Table 2; Fig. 4). Although the small number of females of *G. microtarsus* compromises our statistical analyses, there is a significant difference between males of both species in all remaining traits examined (Table 2), despite a comparable range of age classes.

In terms of qualitative characters, the size of the posterolateral foramina of the palate is comparable to that of the posteromedial vacuities in *G. agilis,* being proportionally larger than in *G. microtarsus* in which they are always smaller than the posteromedial vacuities (Fig. 7). Incipient postorbital processes can be present in both species, contrary to Hershkovitz's (1992) observation that both species lack them.

Conclusion

Gracilinanus agilis and *G. microtarsus* appear to represent valid species, distinguishable by morphological and molecular characters, with levels of sequence divergence equivalent to those separating each of them from a third species, *G. aceramarcae.* In short, these two do not even form a well-supported sister-pair within the genus, even with the very limited number of taxa sampled. However, it is also possible that the samples we allocate to *G. microtarsus* in fact represent two separate species, as indicated by the cyt *b* data. Verification of this hypothesis will have to wait until more samples are available.

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Literature Cited

Bremer, K. 1988. The limits of amino-acid sequence data in angiosperm phylogenetic reconstruction.—Evolution 42:795–803.

Costa, L. P. 2002. Relações filogenéticas intergenéricas de marsupiais didelfídeos. *In* N. C. Cáceres and E. L. A. Monteiro-Filho, eds., Marsupiais Brasileiros Editora da Universidade Federal do Paraná, Paraná (in press).

Creighton, G. K. 1984. Systematic studies on opossums (Didelphidae) and rodents (Cricetidae). University of Michigan, Ann Arbor, 220 pp.

Eisenberg, J. F., & K. H. Redford. 1999. Mammals of the Neotropics: the central Neotropics, vol. 3: Ecuador, Peru, Bolivia, Brazil. The University of Chicago Press, Chicago, 609 pp.

Emmons, L. H., & F. Feer. 1997. Neotropical rainforest mammals: a field guide, 2nd edition. University of Chicago Press, Chicago, 307 pp.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap.—Evolution 39:783–791.

Gardner, A. L. 1993. Order Didelphimorphia. Pp. 15–23 *in* D. E. Wilson and D. M. Reeder, eds., Mammal species of the world. Smithsonian Institution Press, Washington, D.C., 1206 pp.

Gardner, A. L., & G. K. Creighton. 1989. A new generic name for Tate's (1933) *microtarsus* group of South American mouse opossums (Marsupialia: Didelphidae).—Proceedings of the Biological Society of Washington 120:3–7.

Hershkovitz, P. 1992. The South American gracile mouse opossum genus *Gracilinanus* Gardner and Creighton, 1989 (Marmosidae, Marsupialia): a taxonomic review with notees on general morphology and relationships.—Fieldiana: Zoology, New Series 70:1–56.

Kimura, M. 1980. A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences.—Journal of Molecular Evolution 16:111–120.

Papavero, N. 1971. Essays on the history of neotropical dipterology, with special reference to collectors (1750–1905), vol. 1. Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.

Patton, J. L., & L. P. Costa. 2003. Diversidade, limites geográficos e sistemáticos de marsupiais brasilerios. *In* N. C. Cáceres and E. L. A. Monteiro-Filho, eds., Marsupiais Brasileiros. Editora da Universidade Federal do Paraná, Curitiba (in press).

Patton, J. L., M. N. F. da Silva, & J. R. Malcolm. 2000. Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia.—Bulletin of the American Museum of Natural History 244:1–306.

Saiki, R. K., et al. 1988. Primer-directed enzymatic amplification of DNA with a thermostable DNA polymerase.—Science 239:487–491.

Swofford, D. L. 1999. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods), version 4. Sinauer Associates, Sunderland, Massachusetts.

Tate, G. H. H. 1933. A systematic revision of the marsupial genus *Marmosa,* with a discussion of the adaptive radiation of the murine opossums (*Marmosa*).—Bulletin of the American Museum of Natural History 66:1–250.

Vanzolini, P. E. 1993. As viagems de Johann Natterer no Brasil, 1817–1835.—Papèis Avulsos de Zoologia 38(3):17–60.

Voss, R. S., D. B. Lunde, and N. B. Simmons. 2001. The mammals of Paracou, French Guiana, a Neotropical lowland rainforest fauna, part 2. Nonvolant species.—Bulletin of the American Museum of Natural History 263:3–236.

Walsh, P. S., D. A. Metzger, & R. Higuchi. 1991. Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material.—Biotechniques 10:506–513.

Appendix

Gazetteer.—Localities from which we examined material of *Gracilinanus* for this study are listed by species and numbered to correspond with the mapped points in Fig. 1 and the labeled terminals in Fig. 3. Voucher numbers for specimens examined are given parenthetically for each locality; those marked with an asterisk correspond to haplotypes used in the molecular analysis, and boldface place names are used to label the tree. Specimens examined are deposited in the collections of the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Museu de Zoologia da Universidade de São Paulo (MZUSP); Museu Nacional, Rio de Janeiro (MNRJ); and Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais (MCN); and Museo de Historia Natural, Universidad Mayor de San Marcos, Lima, Peru (MUSM). Specimens identified by other prefixes correpond to collector's field number: AP (Adriano Paglia), CEMIG (Luiz Fernando B. M. Silva), RM (Raquel Moura) to be deposited at the Departamento de Zoologia, Universidade Federal de Minas Gerais, Belo Horizonte; LC and LPC (Leonora Pires Costa), LP (Luciana Pereira), UUPI (Maria José de J. Silva) and YL (Yuri Leite) to be deposited at one of the above Brazilian institutions; and UHECO and UHESM (Nelson da Silva) to be deposited at the Universidade Católica de Goiás, Brazil.

Gracilinanus microtarsus

1 Fazenda das Bicas, 7.8 km (by rd.) SSE Lagoa Santa, Minas Gerais, Brazil, 19°38′S, 43°53′W (MNRJ 31445*).

2 Estação de Pesquisas de Peti (CEMIG), 10 km (by rd.) São Gonçalo do Rio Abaixo, Minas Gerais, Brazil, 19°49′S, 43°21′W (MNRJ 31447*, CEMIG 51).

3 Parque das Mangabeiras, Belo Horizonte, Minas Gerais, Brazil, 19°55′S, 43°56′W (MCN 299*).

4 Cruzeiro, 8 km NE Santa Rita de Jacutinga, Minas Gerais, Brazil, 22°5′S, 44°2′W 560 m (LC 1*, LC 2, YL 1).

5 Jurumirim, Minas Gerais, Brazil, 20°8′S, 42°41′W (MCN 394*).

6 Parque Estadual do Rio Doce, 13 km E Marliéria, Minas Gerais, Brazil, 19°43′S, 42°39′W 300 m (MVZ 197587*).

7 Parque do Caraça, 25 km SW Santa Bárbara, Minas Gerais, Brazil, 20°5′S, 43°30′W 1300 m (RM 4*).

8 Floresta Nacional de Ipanema, 20 km NW Sorocaba, São Paulo, Brazil, 23°26′7″S, 47°37′41″W 701 m (LPC 801*, LPC 820–822, MVZ 197463). This is the historical site of "Ypanema", the type

locality of *G. microtarsus*, where the collector, Johann Natterer, lived and worked (see Papavero 1971, Vanzolini 1993), and renamed as a formal conservation unit by IBAMA on May 20, 1992.

9 Fazenda Intervales, Base do Carmo, 5.5 km S Capão Bonito, São Paulo, Brazil, 24°20′S, 48°25′W 700 m (MZUSP 29158–29161, MZUSP 29165, MVZ 182054, MVZ 182055, MVZ 182056*, MVZ 182057).

10 Vila Dois Rios, Ilha Grande, Angra dos Reis, Rio de Janeiro, Brazil, 23°9′S, 44°14′W (LP 40*).

11 Estação Biológica de Boracéia, São Paulo, Brazil, 23°39′S, 45°54′W 850 m (MZUSP 29162, MZUSP 29163*, MZUSP 29164).

Gracilinanus agilis

12 Ponte do Colatino, margem esquerda do Rio Jequitinhonha, Coronel Murta, Minas Gerais, Brazil, 16°36′S, 42°12′W (LC 189*).

13 Vargem do Retiro, Ribeirão Mascates, Parque Nacional da Serra do Cipó, Minas Gerais, Brazil, 19°14′S, 43°33′W 800 m (MNRJ 31396*).

14 Parque Estadual do Rio Preto, 15 km S São Gonçalo do Rio Preto, Minas Gerais, Brazil, 18°9′S, 43°23′W 950 m (YL 64*, LC 71).

15 Fazenda Corredor, Bocaiúva, Minas Gerais, Brazil, 17°22′14″S, 43°52′16″W (AP 22*).

16 Fazenda Santa Rita, 8 km E Andaraí, Bahia, Brazil, 12°48′6″S, 41°15′41″W 399 m (LPC 241*).

17 Mata do Vasco, 12 km W Nova Ponte, Minas Gerais, Brazil, 19°10′15″S, 47°42′29W 878 m (LPC 296–299, LPC 304*, LPC 305–307, LPC 309–311, LPC 314–316, LPC 318, LPC 324, LPC 325, LPC 327–328, LPC 330–331, LPC 339–340, MVZ 197438–197446, 197451–197453, 197473, 197649–197652, 197654–197657).

18 Rio Miranda, above Passo do Lontra, Mato Grosso do Sul, Brazil, 19°34′35″S, 56°55′44″W 100 m (LPC 599*, LPC 602, MVZ 197455).

19 Base de Pesquisa do Pantanal—CENAP/IBAMA, 110 km SSW Poconé, Mato Grosso, Brazil, 17°7′12″S, 56°56′47″W 98 m (LPC 581*, MVZ 197454).

20 Usina Hidrelétrica de Corumbá, 30 km SE Caldas Novas, Goiás, Brazil, 18°0′S, 48°30′W (UHECO 4722*).

21 Fazenda Lagoa Bonita, 36 km N Barra do Garças, Mato Grosso, Brazil, 15°34′50″S, 52°22′29″W 331 m (LPC 476*).

22 Usina Hidrelétrica de Serra da Mesa, Serra da Mesa, Goiás, Brazil, 13°50′S, 48°18′W (UHESM 1759*).

23 Chapada do Araripe, 7 km SW Crato, Ceará, Brazil, 7°16′39″S, 39°27′3″W 960 m (LPC 243, LPC 244, LPC 249, LPC 250*, LPC 251, LPC 269–271, LPC 276–277, LPC 294, MVZ 197447–197450, MVZ 197647–197648).

24 Estação Ecológica de Uruçuí-Una, Piauí, Brazil, 8°50′S, 44°10′W (UUPI 292*).

Gracilinanus aceramarcae

25 Cordillera de Vilcabamba, La Convencíon (Camp 1), Junín, Peru, 11°39′56″S, 73°38′31″W (MUSM 13002*).